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Seasonal body mass changes in Eurasian Golden Plovers *Pluvialis apricaria* staging in the Netherlands: decline in late autumn mass peak correlates with increase in raptor numbers

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Eurasian Golden Plovers *Pluvialis apricaria* staging in the Netherlands during the non-breeding season show strikingly constant seasonal changes in body mass with a first mass peak in late November and December and a second peak in late April and May. Despite huge sample sizes, variations in this pattern over successive years in the 1990s and among age classes were minuscule. However, in contrast to the body mass levels at other times of the year, there was a marked decline in the winter peak mass of Golden Plovers from the 1970s/early 1980s to 1989–2000. The decrease, by an average of 29 g, was about half the extra mass previously stored in autumn. This additional mass is known to consist of fat and may be interpreted as an energy store – insurance – for sudden cold spells when a negative energy balance forces the birds to move south and stay in front of the frostline. As the rate of the mass increase in September–October showed no change from the 1980s to the 1990s, changes in food availability are unlikely to explain the long-term mass decline. Also, there were no differences in two factors known to influence energy expenditure and feeding rate, air temperature and rainfall. The one striking environmental change relevant to plovers was the steep increase in the occurrence of raptors in the northern Netherlands in the 1980s, notably Peregrine Falcons *Falco peregrinus* and Goshawks *Accipter gentilis*. We argue that the halving of the winter mass peak over a decade is consistent with the hypothesis that under increased risk of predation, birds lower their body mass in order to reduce individual vulnerability, a reduction that may be traded off against an increased risk of starvation.

There is increasing evidence that the risk of predation by raptors causes behavioural and physiological adjustments in potential avian victims. For example, the selection of (micro) habitat is shaped by predation risk, as is the degree of flocking and the vigilance behaviour of birds in a flock (e.g. Barnard & Thompson 1985, Lima & Dill 1990, Lindström 1990, Ydenberg 1998, Hilton *et al*. 1999). Changes in body mass as a function of perceived predation risk are particularly interesting as such adjustments directly reflect the trade-off between energy storage to reduce the risk of starvation, and loss of mass to enhance manoeuvrability and reduce the risk of predation (Lima 1986, McNamara & Houston 1990, Witter & Cuthill 1993). So far, most examples of body mass adjustments are from passerines (Gosler *et al*. 1995, Lilliendahl 1997, 1998, 2000, Pravosudov & Grubb 1998, Carrascal & Polo 1999, van der Veen 1999, Gentle & Gosler 2001), but predation risk has been invoked to explain site use and differences in body masses reached by *Calidris* sandpipers at coastal stopover areas (Piersma *et al*. 1993, Lissimore *et al*. 1999).

Eurasian Golden Plovers *Pluvialis apricaria* are common shorebird migrants in grassland areas in the northern Netherlands where they show a clear

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preference for open landscapes. Their flocks avoid proximity to wooded and build-up areas (Jukema *et al*. 2001). The Golden Plovers staging in the Netherlands in autumn, winter and spring, breed in Scandinavia and northern Russia. In October and November many birds move on to wintering areas in western France and the Iberian Peninsula, but some birds remain in the Netherlands and only move to more southern wintering areas when they are pushed by the arrival (usually from the north-east) of frost and snow (Jukema *et al*. 2001). In the course of February, numbers of Golden Plovers build up again before departure in April and May to the boreal and arctic breeding grounds. The populations passing through in autumn and spring consist of the same individuals (Jukema *et al*. 2001).

An old tradition of netting for commercial purposes, the 'wilsternetting', over the past 30 years has been transformed into a monitoring tool during which up to 3000 Golden Plovers annually are captured, aged, ringed and weighed (Jukema *et al*. 2001). Here we first document the seasonal body mass cycle of Golden Plovers staging in the Netherlands. We then compare the mass levels in the 1970s and early 1980s (Jukema 1982) with those in the 1990s, when the weighing of captured birds was resumed after a series of years during which captured birds were only aged and ringed. Finally, the striking difference in peak mass levels in the first and second period will be discussed with reference to possible changes in food availability and predation risk.

METHODS

Eurasian Golden Plovers were captured during daytime at grassland sites in the provinces of Noord-Holland, Friesland and Groningen using so-called 'wilsternets' (Jukema *et al*. 2001). Immediately after capture the plovers were ringed, aged as juvenile (first winter) or adult (older than one year) on the basis of feather characteristics (the presence of secondaries of various ages is especially diagnostic for adults: Jukema *et al*. 2001), and weighed to the nearest gram using Pesola spring-balances. Wing length (maximum chord) was measured on a stopped ruler to the nearest mm. Although wing length explained only 5% of the variance in body mass at a time of year (11 March–10 April) when Golden Plovers are light in weight (Jukema & Piersma 1992), we used wing length as a measure of structural body size. This is because wing length was the only body measure collected by a single observer (Ton Pieters, Waterland), using a constant methodology over a long period.

Total rainfall and air temperature records for the period 21 November–31 December at the De Bilt station were extracted from the monthly reports of the Royal Dutch Meteorological Institute (KNMI, De Bilt). Data on the occurrence of Peregrines were based on (1) an index of the numbers observed during point counts in the provinces of Noord-Holland, Friesland and Groningen in December (SOVON pers. comm.) and (2) numbers encountered during high-tide shorebird and raptor counts along the Friesian coast in November and December (Engelmoer *et al*. 1996).

RESULTS

Over the years 1989–2000, body mass values of Golden Plovers ranged between individual minimum masses of 140 g in autumn and spring, and maximum masses of 290 g in November (Fig. 1A). Despite this large overall variation, the body mass values per 10-day period were normally distributed (e.g. means and medians almost always coincided) and were tightly centred around the means (50% of the data were always contained in 20-g intervals around the mean). However, there were clear seasonal changes in body mass, with a first broad peak from mid November extending into December and early January and a second peak in late April extending into May. The differences in body mass values between birds identified as juveniles and adults were small (Fig. 1B). An analysis of variance (Table 1) demonstrates that age, although a significant factor, explained 1% or even less of the variance in body mass values. This was also true for year-to-year variations in body mass. Based on the relatively large

Figure 1. (A) Seasonal changes in body mass of Eurasian Golden Plovers in the Netherlands 1989–2000. The numbers indicate total sample sizes recorded per 10-day period. (B) Absence of differences in average body mass levels of juvenile (first winter) birds and adults in the years 1989–2000. (C) Comparison of the seasonal changes in average body mass of both age categories of Golden Plovers in an early period (1970s–early 1980s, open symbols) and a late period (1989–2000, closed symbols). Data collected by J.J. in the period 1976–84 are indicated by open circles (the numbers indicating total sample sizes), whereas the two triangles indicate average body mass values reported for 21 Golden Plovers captured on a Friesian saltmarsh in December (*c.* 1970) by Eenshuistra (1973) and 194 Golden Plovers captured in peatland meadows in Noord-Holland just north of Amsterdam from 21 November to 31 December 1977–84 (T. Pieters pers. comm.).

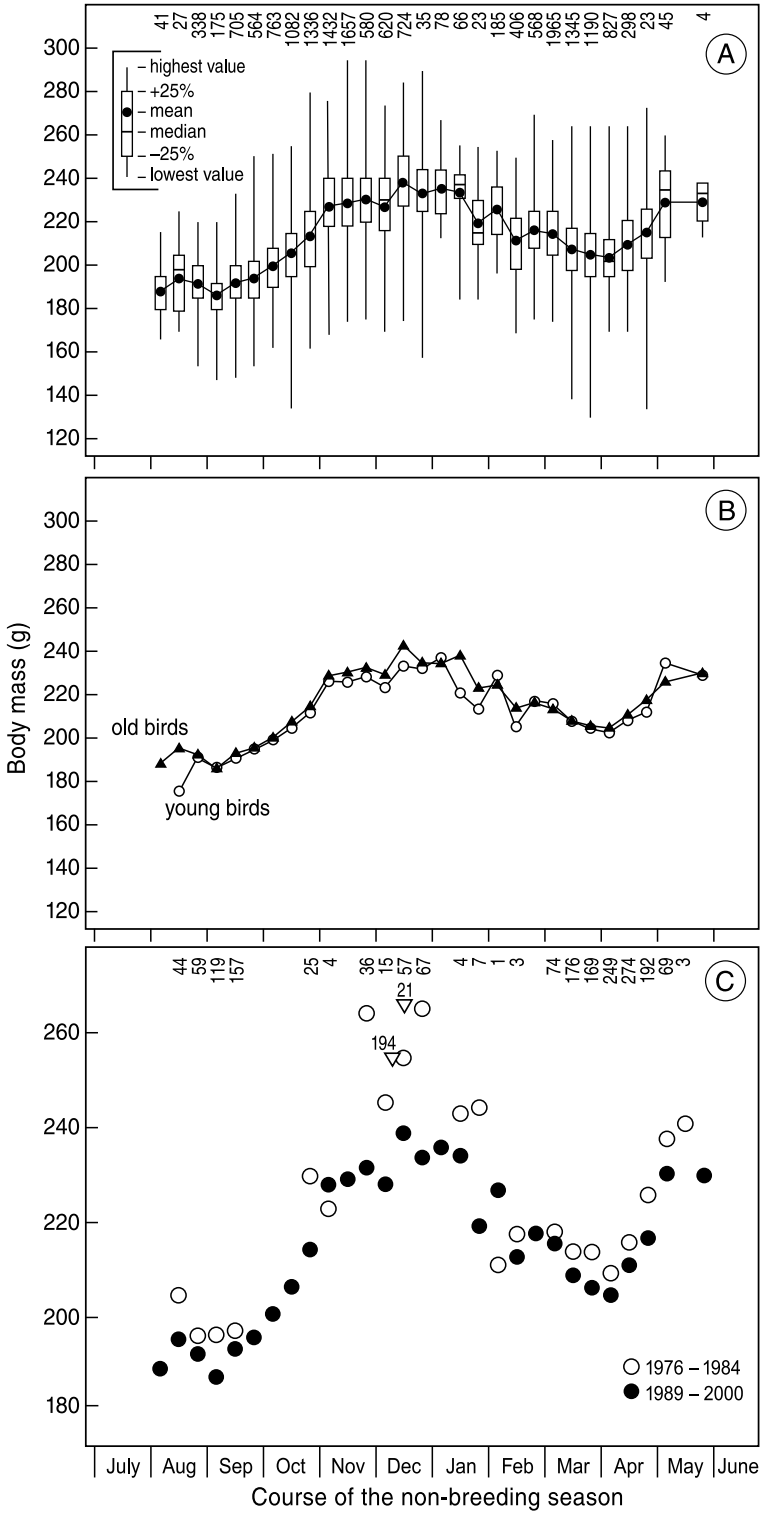
41 27 338 175 705 564 763 1082 1336 1432 1657 580 620 724 35 78 66 23 185 406 568 1965 1345 1190 827 298 23 45 4
A
highest value
+25%
mean
median
–25%
lowest value
300
280
260
240
220
200
180
160
140
120
B
Body mass (g)
old birds
young birds
44 59 119 157 25 4 36 15 57 67 4 7 1 3 74 176 169 249 274 192 69 3
C
21
194
260
240
220
200
180
1976 – 1984
1989 – 2000
July Aug Sep Oct Nov Dec Jan Feb Mar Apr May June
Course of the non-breeding season

Table 1. Analysis of variance of body mass of 18 120 non-breeding Eurasian Golden Plovers captured in August–May in the northern Netherlands in 1989–2000 (see Fig. 1). In this model, which explained 40% of the variance in the dependent variable (body mass), Month, Year and Age are category variables. The two- and three-way interactions were not significant and were excluded from the model

Independent variables	*df*	Sum of squares	*F*-ratio	*P*
Month	9	2 812 500	1251.1	<0.0001
Year	11	62 106	22.6	<0.0001
Age	1	46 397	185.8	<0.0001
Error	18 098	4 520 410		

sum-of-squares, season (i.e. the category variable 'Month') explained most, by far, of the total variance (40%) for the period 1989–2000 (Table 1). This indicates that Golden Plover body mass varied seasonally in an extremely consistent manner.

Yet, when the mass values from 1989 to 2000 are compared with body mass data collected from 1976 to 1984 in inland meadows in northern Friesland (Jukema 1982; Fig. 1C), the much higher average body mass values reached in mid November and December in the earlier period are striking. Using the five averages for 10-day periods (mid November–December) from the two data sets, the difference between mass peak levels in 1976–84 (averages for four winters available) and 1989–2000 (averages for five winters available) is significant (pooled-variance Student's *t*-test, $t_7 = 5.40$, $P = 0.001$). These high peak body mass values were also found by Eenshuistra (1973; Fig. 1C) for Golden Plovers captured on the Friesian saltmarshes and in a sample of birds from a completely different habitat, the peatland meadows north of Amsterdam (Fig. 1C). In 1989–2000, the average body mass in the last 20 days of November and in December was 231 g, whereas the weighted average across all samples collected from 1970 to 1984 was 260 g. This difference of 29 g is about half of the mass increment in autumn before the 1970s/early 1980s.

In order to rule out the possibility that this difference was caused by changes in structural body size (Piersma & Davidson 1991), we compared wing length measurements collected during the two periods. The average wing length in 1976–84 was 192.0 mm ($n = 763$, sd = 4.6) and in 1989–98 it was 190.7 mm ($n = 22$, sd = 4.4), a difference that is not only small but also not statistically significant (pooled-variance Student's *t*-test, $t = 1.249$, $P = 0.212$).

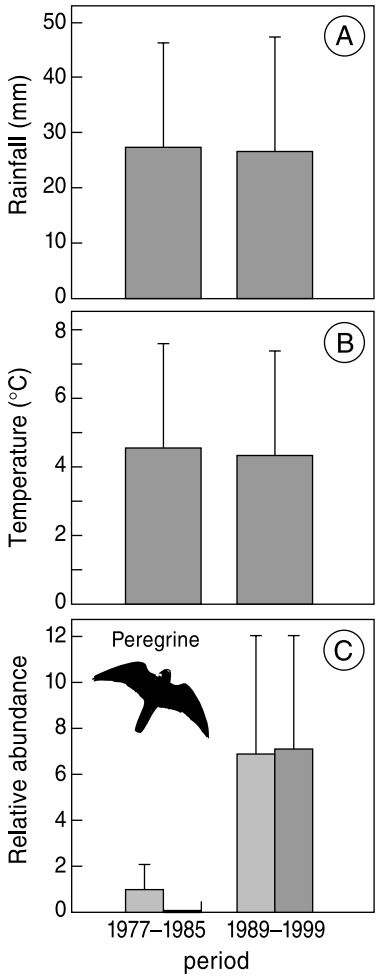

Figure 2. (A,B) Changes between the periods 1977–85 and 1989–99 in two environmental parameters [(A) rainfall and (B) air temperature] and (C) the incidence of observations of Peregrine Falcons from a point-counting scheme in the northern Netherlands (left column) and high-tide roost counts in Friesland (right column). In all three graphs, the vertical lines above the bars indicate sd calculated on the basis of among-year variation. Using *t*-tests, the differences in Peregrine numbers for both data sets are significantly different between the two periods (for the left column, a separate variance *t*-test indicates $t_{15} = 2.74$, $P = 0.015$; for the right column, a one-sample *t*-test against a value of 0 indicates $t = 5.93$, $P = 0.001$).

With respect to possibly critical environmental factors discussed further below, rainfall in late November and December showed no difference between the first and the second period (Fig. 2A). Air temperatures also were similar throughout the period covered by this study (Fig. 2B). However, according to two independent monitoring schemes, Peregrine Falcons *Falco peregrinus* increased by a factor of seven or more between the periods 1977–85 and 1989–99 (Fig. 2C).

DISCUSSION

The (early) winter peak in body mass of Golden Plovers is typical for shorebirds wintering at temperate latitudes (Johnson 1985, Zwarts *et al*. 1996). It also occurs in some other waterbird groups (e.g. Piersma 1988) and in passerines (e.g. King & Farner 1966, Blem 1976, Lehikoinen 1987). It is generally accepted (e.g. Biebach 1996) that such 'winter fattening' is an energy storage strategy used to overcome periods without food, whether such spells are as predictable and short as one night (as in the case of diurnally feeding passerines) or unpredictable and lasting one or more days (as during bad weather periods when food intake is reduced and/or energy expenditure increased). In the case of Golden Plovers the additional winter mass, which is known to consist entirely of fat (Piersma & Jukema 2002), may indeed be interpreted as an energy store for the sudden cold spells when a negative energy balance forces the birds to move south or south-west several 100 km and stay in front of the frostline (Jukema *et al*. 2001). But why would Golden Plovers reduce this strategic energy store by half over a period of *c.* 10 years?

As we have seen, there is no evidence that there have been changes in the body size of the plovers staging in the Netherlands in late November/December. Over the period of study there were no detectable changes in the migration destinations in winter, nor in the general lifecycle characteristics of Golden Plovers in the Netherlands either (Jukema *et al*. 2001). Two likely explanations remain: (1) the proximate (mechanistic) explanation that food availability and feeding conditions have declined to such an extent that deposition of the peak masses by increased energy intake can no longer be achieved; and (2) the ultimate (functional) explanation that the relative risks of predation and starvation have changed in such a way that the optimal energy store has recently become much lower than before.

The fact that the rates of body mass gain in September and October were similar in the early and late period (Fig. 1C) argues against the idea (1) that energy intake rates have decreased as a consequence of changing food conditions. Also, the weather factor that most strongly influences surface activity of their staple food (earthworms, Lumbricidae; Byrkjedal & Thompson 1998), i.e. rainfall (MacDonald 1983), did not change with time (Fig. 2A), and, with regard to explanation (2), neither did the air temperature (Fig. 2B). There were no differences in minimum air temperatures or overall winter severity between the periods either. All of this argues against the idea that the risk of starvation resulting from inclement weather (i.e. by increasing daily energy expenditure) has changed.

However, it is possible that the risk of predation has increased considerably, as the numbers of Peregrine Falcons, probably the most dangerous predator for Golden Plovers, increased considerably. Another potential predator that over the last 30 years has expanded to areas traditionally frequented by non-breeding Golden Plovers is the Goshawk *Accipiter gentilis* (Bijlsma 1993, Bijlsma *et al*. 2001). In 1973–77 only one to three pairs of Goshawks defended year-round territories in the province of Friesland. This number increased to 15–30 territories in 1977–88, 75–90 territories in 1989–92 and 125–135 territories in 1995–99 (R.G. Bijlsma pers. comm.). Although Goshawks still breed in woods, areas Golden Plovers tend to avoid (Bijlsma *et al*. 2001), even in early summer when Golden Plovers occur north of the Netherlands, feather-remains of Golden Plovers have been found at Goshawk nests (R.G. Bijlsma pers. comm.). Finally, reflecting the increase of several species of raptor in northern Europe (Bijlsma 1993, Koks 1998, Kjellén & Roos 2000), local though less pronounced increases have also been reported for passing Merlin *Falco columbarius* and Sparrowhawk *Accipiter nisus* (Engelmoer *et al*. 1996, Jukema *et al*. 2001). Although both of these raptors usually select prey smaller than Golden Plovers, they remain a potential threat for these waders (e.g. Cresswell 1995). On the island of Texel, Sparrowhawks as well as Goshawks have repeatedly been observed as they attacked Golden Plover flocks (pers. obs.).

Perhaps owing to the particularities of the system, Whitfield *et al.* (1999) were unable to establish that a raptor like the Eurasian Sparrowhawk selectively preyed upon the fattest Redshanks *Tringa totanus* present. Nevertheless, many studies have now established that increased body mass leads to reduced take-off speed (Metcalfe & Ure 1995, Kullberg *et al*. 1996, Veasey *et al*. 1998, Lind *et al*. 1999) and manoeuvrability in flight (Witter *et al*. 1994). For this reason, a reduced fat store will enhance an individual plover's capacity to escape attacking Peregrines and hawks. Furthermore, a reduction in fat storage before mid winter might reduce the time requirement for intense feeding, i.e. times when the ability to detect and identify predators may be compromised (e.g. Barnard & Thompson 1985). That the peak body mass reduction correlates with a strong numerical increase in what is probably the most dangerous avian predator, is thus consistent with the idea that the perceived predation risk is traded off against the

risk of starvation by a strategic lowering of body mass (as found by, e.g. Gosler *et al.* 1995, van der Veen 1999, Lilliendahl 2000, Gentle & Gosler 2001).

We suggest that Golden Plovers staging in the Netherlands in the 1980s have reduced their strategic fat store in late November and December in response to a strongly increased perceived risk of predation. This fat store enables them to overcome the first cold spells of winter and fly the short distances to frost-free areas in western France, south and south-west of the Dutch staging areas (Jukema *et al.* 2001), but the ring-recovery patterns do not indicate that the length of this early winter migration has reduced (E.J. Bunskoeke pers. comm.), as would be expected. The weakness of our hypothesis is that it effectively hinges on a single comparison. Unlike Gosler *et al.* (1995), we are unable to perform a multiple comparison that includes periods with a constant, declining and increasing predator presence. However, our hypothesis may be evaluated with time series of body masses from a range of shorebird species, especially if they differ in vulnerability to predation. In addition, field studies on the hunting styles of raptors (e.g. Bijlsma 1990) and other details of the predator–prey interactions in the raptor–shorebird system are pertinent (Lima 2002).

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